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Spider Systematics: Past and Future

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Spider systematics has a history that reaches back over 250 years, to the publication of Carl Clerck's *Svenska Spindlar* (Clerck, 1757). Linnaeus (1758), in the famous 10th edition of his *Systema Naturae* that was published the following year (and which serves as the starting point for the rest of zoological nomenclature), recognized only 39 species of spiders, worldwide, even though he knew (and cited) Clerck's book. Clerck had already recognized more species than that from Sweden alone, and (unlike Linnaeus) provided good, color illustrations of them, often including even drawings of the male palps. So it is not surprising that arachnologists take Clerck, rather than Linnaeus, as their starting point.

The most current version, 13.5, of the World Spider Catalog (Platnick, 2013) lists a total of 43,678 currently valid species, placed in 3,898 genera and 112 families (Table 1). The database version of the catalog has recently been updated to include the information from version 11.0 of the text catalog (previously, only the information from version 8.5 was accessible in database form). The relational database version is managed in R:base 9.1 Extreme (www.rbase.com); data were converted from the original XyWrite III+ files, and the family and other statistics checked back against those original files. The names of authors, journal titles, and distributions were normalized, with distributions coded into seven biogeographic regions (Australian, Palearctic, Nearctic, Ethiopian, Oriental, Indian, and Neotropical). The availability of the updated database, covering the literature through mid-2010, allows us to make some observations about the progress of spider systematics, from Clerck to the present. Although the data allow us to determine whether species were first described from males only, females only, both sexes, or only from juveniles, they do not allow us to determine whether species were described from more than a single male and/or female specimen.

TABLE 1. Currently valid spider families, genera, and species (as of Dec. 13, 2012).

Family#	Family	Genera	Species	#	Family	Genera	Species
1	Liphistiidae	3	90	59	Anapidae	38	153
2	Atypidae	3	49	60	Micropholcommatidae	19	66
3	Antrodiaetidae	2	33	61	Mysmenidae	23	123
4	Mecicobothriidae	4	9	62	Synaphridae	3	13
5	Hexathelidae	12	112	63	Pimoidae	4	37
6	Dipluridae	24	179	64	Sinopimoidae	1	1
7	Cyrtaucheniidae	10	102	65	Linyphiidae	590	4429
8	Ctenizidae	9	128	66	Tetragnathidae	47	957
9	Euctenizidae	7	33	67	Nephilidae	4	61
10	Idiopidae	22	314	68	Araneidae	170	3037
11	Actinopodidae	3	40	69	Lycosidae	120	2393
12	Migidae	10	91	70	Trechaleidae	16	119
13	Nemesiidae	43	364	71	Pisauridae	48	331
14	Microstigmatidae	7	16	72	Oxyopidae	9	444
15	Barychelidae	44	307	73	Senoculidae	1	31

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TABLE 1. (Continued)

Family#	Family	Genera	Species	#	Family	Genera	Species
16	Theraphosidae	124	946	74	Stiphidiidae	22	135
17	Paratropididae	4	8	75	Zorocratidae	5	42
18	Hypochilidae	2	12	76	Psechridae	2	51
19	Austrochilidae	3	9	77	Zoropsidae	14	86
20	Gradungulidae	7	16	78	Zoridae	14	79
21	Filistatidae	17	112	79	Ctenidae	40	480
22	Sicariidae	2	127	80	Agelenidae	68	1153
23	Scytodidae	5	228	81	Cybaeidae	10	177
24	Periegopidae	1	2	82	Desidae	38	181
25	Drymusidae	1	16	83	Amphinectidae	32	159
26	Leptonetidae	22	271	84	Cycloctenidae	5	36
27	Telemidae	8	61	85	Hahniidae	27	247
28	Ochyroceratidae	14	161	86	Dictynidae	51	575
29	Pholcidae	90	1330	87	Amaurobiidae	52	285
30	Plectreuridae	2	31	88	Phyxelididae	14	64
31	Diguetidae	2	15	89	Titanoecidae	5	53
32	Caponiidae	15	84	90	Nicodamidae	9	29
33	Tetrablemmidae	30	144	91	Tengellidae	9	57
34	Trogloraptoridae	1	1	92	Miturgidae	28	369
35	Segestriidae	3	119	93	Anyphaenidae	56	519
36	Dysderidae	24	526	94	Liocranidae	31	204
37	Oonopidae	89	1033	95	Clubionidae	16	582
38	Orsolobidae	29	184	96	Corinnidae	87	1032
39	Archaeidae	4	70	97	Zodariidae	78	1068
40	Mecysmaucheniidae	7	25	98	Penestomidae	1	9
41	Pararchaeidae	7	35	99	Chummidae	1	2
42	Holarchaeidae	1	2	100	Homalonychidae	1	3
43	Huttoniidae	1	1	101	Ammoxenidae	4	18
44	Stenochilidae	2	13	102	Cithaeronidae	2	7
45	Palpimanidae	15	131	103	Gallieniellidae	11	57
46	Malkaridae	4	11	104	Trochanteriidae	19	152
47	Mimetidae	13	156	105	Lamponidae	23	192
48	Eresidae	9	95	106	Prodidomidae	31	304
49	Oecobiidae	6	110	107	Gnaphosidae	118	2134
50	Hersiliidae	15	176	108	Selenopidae	10	239
51	Deinopidae	2	60	109	Sparassidae	85	1135
52	Uloboridae	18	266	110	Philodromidae	29	538
53	Cyatholipidae	23	58	111	Thomisidae	174	2151
54	Synotaxidae	14	82	112	Salticidae	591	5570
55	Nesticidae	9	209				
56	Theridiidae	121	2351		Total	3898	43678
57	Theridiosomatidae	16	89				
58	Symphytognathidae	7	66				

If you simply parse the list of currently valid species by author, it turns out that the 10 most prolific authors have jointly described almost one-third of the total: Eugène Simon leads the list by far, having described 3,789 of the currently valid spider species, followed by Norman Platnick (1,828), Herbert Levi (1,268), Tamerlan Thorell (1,168), Embrik Strand (1,097), Candido de Mello-Leitão (1,056), Willis Gertsch (998), Ralph Chamberlin (984), Octavius Pickard-Cambridge (932), and Raymond Forster (847), totaling 13,929 (figures for the two living authors have been updated to the middle of 2013). However, these are raw counts, not corrected for co-authorship, so that species co-authored, for example by Platnick and Forster, or by Gertsch and Chamberlin, are included twice. Rather than attempting to apportion the counts among those co-authors, adding the next two most prolific workers (Eugen von Keyserling, with 827 currently valid species, and Ludwig Koch, with 727) brings the joint total to over 15,500, easily more than one-third of all the currently valid species. To take the listing up to half the currently known species, you would need to add at least another 15 authors.

Of course, these counts of currently valid species do not tell the whole story. Some of these authors also described fair numbers of species that have already been synonymized—i.e., shown to have been described earlier by someone else (or even by themselves!)—or formally determined to be unrecognizable (i.e., placed as nomina dubia). The total number of synonyms created while describing these 15,500 spider species is appallingly high, but shows definite changes over time. One can easily compute the percentage of the total number of species described by each author that are still valid:

Most Prolific Authors of Spider Species

author	#currently valid	#syns/dubia	#total	%still valid
Simon	3789	861	4650	81.5
Platnick	1828	3	1831	99.8
Levi	1268	49	1317	96.3
Thorell	1168	330	1498	78.0
Strand	1097	446	1543	71.1
Mello-Leitão	1056	417	1473	71.2
Gertsch	998	176	1174	85.0
Chamberlin	984	491	1475	66.7
O. Pickard-Cambridge	932	470	1402	66.5
Forster	847	5	852	99.4
Keyserling	827	282	1109	74.6
L. Koch	727	211	938	77.5
Total	15,521	3,741	19,262	80.6

If you look at the bottom line, there is a 20% slop in the system, but that is largely a historical artifact. There is actually a fairly sharp break in these figures. Eight of these 12 authors were working when most taxonomic papers were faunistic in nature, just describing species from a limited geographic area. That is a fairly sloppy procedure, and if you compute the totals for just those eight authors, species that are still valid comprise only about 75% of their joint total. In other words, one-quarter of their efforts were largely wasted, because geographically-limited approaches entail other serious limitations.

About 50 years ago, spider systematics moved from being largely faunistic to largely revisionary, so that the best (and most productive) taxonomists turned their attention to doing comprehensive studies of particular taxa, throughout their distribution. Willis Gertsch's career, for example, bridged that transformation. Most of his faunistic work was done early in his career, and his figure is up to 85%. The more recent, thoroughly monographic workers are all over 96%, perfectly acceptable, even acknowledging that there has been less time for other workers to find any new synonyms these folks may have created. By its nature, revisionary work is far more likely to discover synonyms than to create them, so we do not expect the percentages of valid taxa described by the recent, monographic workers to decrease significantly in the future.

We might reasonably ask, "What made these people successful"? If we go to the top of the class, and look first at Simon, then clearly it does not hurt to be born independently wealthy! Simon was rich enough that he did not have to be an employee of the Muséum National d'Histoire Naturelle in Paris, where he spent his career, and he was able to finance

his own collecting expeditions (for example, to Venezuela and the Philippines) at a time in the 19th century when such expeditions were neither simple nor quick. Simon is clearly the towering figure in the history of spider systematics. Some 20% of the currently valid genera were first described by Simon, and his monumental, four-volume treatise on the *Histoire Naturelle des Araignées* remains the classic work covering all spiders, worldwide.

Simon's career also shows us some other keys to success. First, you need to start early! In Simon's case, his first publication was a 540-page book on the natural history of spiders. Simon produced that book at the age of 16, and the most productive arachnologists did tend to produce their first publications at an early age (ranging up to 31, with an average age of less than 25). But starting early is not enough; you also need to live a long time! The statistics on the publishing careers of these people are amazing, averaging well over 45 years:

author	age at first publication	career span	career years
Simon	16	1864-1923	59
Platnick	20	1972–present	40+
Levi	30	1951–present	60+
Thorell	24	1854–1910	56
Strand	22	1898–1936	38
Mello-Leitão	29	1915–1951	36
Gertsch	22	1928–1986	58
Chamberlin	25	1904–1958	54
O. Pickard-Cambridge	31	1859–1914	55
Forster	21	1949–1999	50
Keyserling	29	1862–1893	31
L. Koch	30	1855–1882	27

Note, however, that they were not typically monomaniacal; indeed, many of these folks also worked on other groups of organisms (Simon, for example, published on hummingbirds; Gertsch also worked extensively on scorpions, as did Chamberlin on myriapods, and Forster on opilionids).

Recent years have seen a remarkable increase in the total number of publishing arachnological systematists; if one counts simply the number of different authors contributing currently valid species in a given year, it took over a century, to 1871, before that number reached 10. Doubling the number to more than 20 took until 1932; doubling it again, to more than 40, took until 1978, and 80+ was not reached until 1989. In the years since 1989, the number of workers has averaged almost 120, with the maximum, of 168, in 2008.

The species accumulation curve shows a similarly impressive trajectory (Fig. 1). Clerck's starting point (53 currently valid species, published in 1757) was not equaled again until 1833. The addition of 200 or more currently valid species in a single year did not occur until 1846, nor again until 1872. The ensuing four decades (1872 through 1911) added an average of over 286 currently valid species per year, clearly reflecting Simon's most productive years. The annual increase did not reach that high again until 1929, and did not consistently reach that level again until 1978. Over the two decades from 1980 through 1999, the average reached almost 435 species per year, and over the last decade, from 2000 through 2009, the average has been over 605 new species per year. During the period from 2000 through mid-2010, 6,396 new species descriptions appeared in 250 different journals, but over half the total appeared in just 14 journals, with the largest numbers appearing in the *Bulletin of the American Museum of Natural History* (777) and *Zootaxa* (605). Only three other journals contributed more than 200 species (*Arthropoda Selecta* with 269, *Journal of Arachnology* with 226, and *Bulletin of the British Arachnological Society* with 204).

The combination of these two trajectories, however, means that there have been significant changes in the average number of species contributed per worker/year. During the four decades of the classical period, from 1872 through 1911, on average each worker added over 26 species per year to the total. Over the last decade, from 2000 through 2009, the average per worker has never reached 8 species per year, and has usually been under 6 species per year (see the similar calculations in Joppa et al., 2011). Of course, today's species descriptions are far more demanding than were those of early arachnologists, providing vastly more information per species. Simon's species descriptions, for example, typically consisted of just a few lines of text and no illustrations, and those species usually can be identified only by reference to their type specimens, not from their original descriptions.

Over the last decade, faunistic work has been responsible for much of the total increase in species numbers. Although this reflects a healthy growth in our knowledge of the faunas of some geographic areas that were scarcely

touched during the classical period, the lesson of history looms large. Faunistic work is highly inefficient and inaccurate; it leads to a substantial waste of effort, and not simply by the faunistic workers who are often contributing synonyms and misplaced species because they do not have adequate knowledge of taxa from other places. Their work also adds to the burden of revisionary systematists, who must spend their time correcting the mistakes made in faunistic studies. Clearly, that burden is exacerbated by the policies of funding agencies that are loath to support research that crosses their national boundaries. In the face of the costs of dealing with invasive species, globally, such xenophobia is surely myopic.

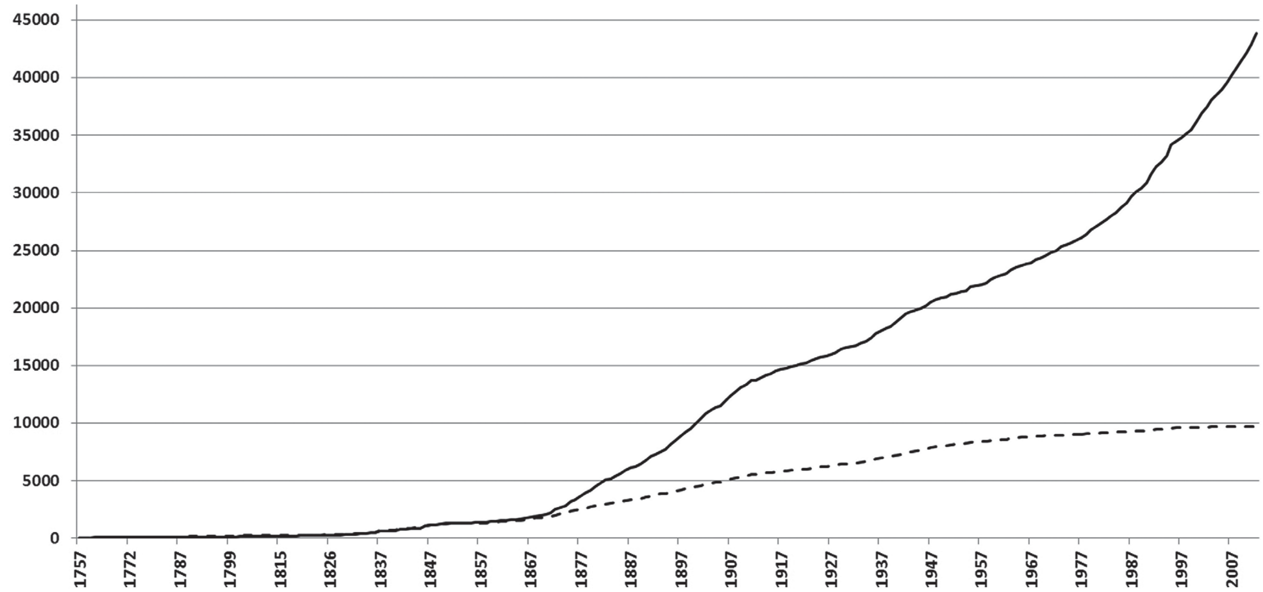

FIGURE 1. Species accumulation curves for currently valid spider species, from Clerck to present (solid line) and for currently invalid names (dashed line).

The increasing threshold of work required to adequately document new species is unfortunately at odds with current measures of the impact factors of scientific papers. Although excellent taxonomic papers have an extraordinarily long shelf-life, and may be cited for many decades, they typically do not receive high numbers of citations in the months immediately following their publication. Unfortunately, even these excellent papers are often not cited by the biologists who use them to identify their study taxa. For small faunistic papers, the outlook is even worse; some of those papers do not even meet the threshold for inclusion in the World Spider Catalog, which requires the presence of taxonomic novelties (new taxa, transfers, or synonymies) or useful genitalic illustrations before a paper is cited.

Of course, the existence of a currently valid name does not mean that a species is well known, much less correctly placed; for example, only about 53% of the species valid in 2010 are known from both sexes. In many spider groups, male palpal characters provide the best features for diagnosing species and identifying new specimens, and that is reflected in the success rate of descriptions. For the 2010 figures, only 41,719 of the 51,227 described species remained currently valid, so only 81% of the proposed names survived (a species accumulation curve for the currently invalid taxa is also shown in Fig. 1); for the 23,145 names originally based only on females or juveniles, the success rate was even lower, 77%. Interestingly, the percentage of species originally described from both sexes varies significantly by geographic region; the highest rates of complete descriptions (both sexes) are from the Nearctic (77%), Palearctic (66%), and Australian (54%) regions, with the remaining regions ranging from 39–49%.

The relatively high synonymy rate characterizing the classical spider literature is easily explained. In those times, type specimens were usually available only to the original authors, and published descriptions were almost always inadequate for identification (no fewer than 12,649 names were proposed with no accompanying illustrations at all!). These factors account for the low success of some classical studies; of the eight new species described by Rossi (1790), for example, only two are still considered valid. That some recent papers show similarly poor success rates seems to be due primarily to faunistic approaches, with species being described multiple times from nearby countries. For example, Tang & Li (2009) described a new genus of crab spiders, including three new species, from China, but Benjamin (2013) showed that the genus had already been described from Indonesia by Thorell over a century earlier, and that two of the three newly proposed specific names are merely synonyms of species that were described earlier from Vietnam and Sumatra.

In the case of these crab spiders, one could argue that the lack of success should be attributed to Thorell, who (in his typical style) provided a lengthy verbal description of the type species, but no illustrations. That was an ineffective

strategy on his part, which highlights the importance of making today's illustrations freely available online. But the onus is clearly on modern workers who, in describing a new genus, need to accurately differentiate their taxon from all the previously described genera in the family, not just some of them. Reviewers of such manuscripts should require that this "burden of proof" be met.

Opinions vary on how large a proportion of the world's spider fauna is actually known at this point, but even the rosiest of calculations suggest that we are only halfway through the task of describing all the world's spiders (e.g., Platnick, 1999). If we still need to describe 40,000 species, and we are currently averaging only 605 per year, then it will likely take us at least another 66 years to accomplish the task; if you factor in the clean-up work that will be required to fix faunistic flaws, the span is probably 80 years, at least. If we accept instead the estimates by other workers (e.g., Agnarsson et al., 2013) that only 35% of the world's spider fauna has been described to date, and if synonymy rates do not improve, then we are probably looking at over 150 years of work, at current rates.

Given the dimensions of the world's current biodiversity crisis, this is not a healthy prospect; far too many spider species are likely to go extinct before they are even discovered. Here again, history is relevant. Platnick's career, for example, was successful not because of independent wealth, but because he had available support staff who could help with the sizable tasks of curating and imaging the relevant collections of specimens, as well as (in recent years) cyberinfrastructure that has enabled him to work efficiently with collaborators. The recipe for success, it seems, would be to identify some 25 young, talented systematists with an abiding interest in spiders, provide each of them with an adequate support staff (including a field assistant, a collection manager, and an imaging technician), equip them with cyberinfrastructure that enables them to function as a cohesive workforce, and continue that support throughout their entire professional careers. With such a workforce, we believe the task could be largely completed in a single generation.

We estimate that the current cost of funding such a four-person lab would be about US $500K per year, including salaries, benefits, equipment, supplies, and fieldwork, in which case supporting such a lab for 40 years would cost around $20 million and supporting 25 such labs, globally, for the same period would cost around $500 million. That amount is certainly dwarfed by the vast economic potential of spider silks and venoms, to say nothing of the economic benefits of the ecosystem services spiders provide as predators of insect pests.

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